Choice of baseline climate data impacts projected species' responses to climate change

Running head: Baseline climate data uncertainty

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Abstract

Climate data created from historic climate observations are integral to most assessments of potential climate change impacts, and frequently comprise the baseline period used to infer species-climate relationships. They are often also central to downscaling coarse resolution climate simulations from General Circulation Models (GCMs) in order to project future climate scenarios at ecologically relevant spatial scales. Uncertainty in these baseline data can be large, particularly where weather observations are sparse and climate dynamics are complex (e.g. over mountainous or coastal regions). Yet, importantly, this uncertainty is almost universally overlooked when assessing potential responses of species to climate change. Here we assessed the importance of historic baseline climate uncertainty for projections of species' responses to future climate change. We built species distribution models (SDMs) for 895 African bird species of conservation concern, using six different climate baselines. We projected these models to two future periods (2040-2069, 2070-2099), using downscaled climate projections, and calculated species turnover and changes in species-specific climate suitability. We found that the choice of baseline climate data constituted an important source of uncertainty in projections of both species turnover and species-specific climate suitability, often comparable with, or more important than, uncertainty arising from the choice of GCM. Importantly, the relative contribution of these factors to projection uncertainty varied spatially. Moreover, when projecting SDMs to sites of biodiversity importance (Important Bird and Biodiversity Areas), these uncertainties altered site-level impacts, which could affect conservation prioritisation. Our results highlight that projections of species' responses to climate change are sensitive to uncertainty in the baseline climatology. We recommend that this should be considered routinely in such analyses.

Introduction

The effects of climate change on the distribution and abundance of species are already being observed (Chen *et al.*, 2011; VanDerWal *et al.*, 2013), with increasing evidence of long-term climate trends driving changes in populations across a range of ecological systems (Cahill *et al.*, 2013). Climate change, along with changes in patterns of land use, is likely to be a major driver of biodiversity loss over the coming centuries. Species with narrow climate tolerances and low capacity to adapt to novel conditions are likely to be particularly affected (Foden *et al.*, 2013). Consequently, a major conservation priority is to develop an understanding of how populations are affected by climate variability and long-term change (Ockendon *et al.*, 2014; Pearce-Higgins *et al.*, 2015), and to develop modelling frameworks to predict potential climate change impacts on biodiversity in order to inform conservation management (e.g. Kearney & Porter, 2009; Dullinger *et al.*, 2012; Foden *et al.*, 2013).

The dominant methodological approach used to assess potential climate change impacts on species has been the development of statistical models that aim to describe a species' relationship (in terms of, for example, distribution or abundance) to climate (Pacifici *et al.*, 2015). These correlative species distribution models (SDMs) can be used in conjunction with simulated future climate data to project likely responses to climate change (Elith & Leathwick, 2009). Such models are primarily aimed at assessing likely geographical shifts in climate suitability (Willis *et al.*, 2015) and, in their simplest form, do not directly consider species-specific traits that might affect climate change vulnerability (e.g. dispersal ability or demography). As a consequence, other approaches have been developed that attempt to directly incorporate demographic processes (Dullinger *et al.*, 2012), physiological limits (Kearney *et al.*,

2008) and species-specific traits (Foden *et al.* 2013) into assessments of future climate change impacts on species.

When evaluated, uncertainty in projected species responses to climate change (e.g. range shifts, changes in abundance) tend to be high, with the dominant sources of uncertainty including variability among future climate projections, modelling methodologies, choice of climate predictor variables and the underlying biodiversity data (Dormann *et al.*, 2008; Buisson *et al.*, 2010; Synes & Osborne 2011; Cheaib *et al.*, 2012; Bagchi *et al.*, 2013). Most studies quantify uncertainty from choices made during the modelling processes, for example, by using future climate projections derived from several different General Circulation Models (GCMs) and using multiple SDM techniques (Araújo *et al.*, 2011; Garcia *et al.*, 2012). The range of responses that might result from different future greenhouse gas emissions scenarios is frequently assessed using data from GCMs run under multiple scenarios. These projection ensembles can then be used to estimate the likely range of species or community responses to climate change across the range of known uncertainty (Araújo & New, 2007; Bagchi *et al.*, 2013; Baker *et al.*, 2015). However, much methodological and data uncertainty remains unaccounted for in such model ensembles, including biological effects (Willis *et al.*, 2015). The influence of this uncertainty on projections of species' responses to climate change and the effectiveness of conservation planning is itself uncertain (Carvalho *et al.*, 2011; Kujala *et al.*, 2013).

Historic gridded climate data, often referred to as 'observational' data, are central to many ecological studies, for example, to assess the importance of climate variability

100 on population dynamics (e.g. Gregory *et al.*, 2009) or for building models to project
101 future impacts (e.g. Bagchi *et al.*, 2013). Historic gridded climate data are also often
102 central to the process of downscaling coarse resolution climate simulations from
103 GCMs (typically available at 100-300km resolution) to scales of ecological relevance
104 (typically 50km resolution or finer). The simplest and most frequently used
105 downscaling approaches (e.g. statistical downscaling and the change factor method,
106 CFM) apply change in a given variable simulated by the GCM, e.g. temperature or
107 precipitation, to a finer resolution baseline climate (Wilby & Wigley, 1997; Tabor &
108 Williams, 2010). This results in climate data with a higher spatial resolution than the
109 GCM, although the underlying simulation of climate change is influenced only by
110 coarse-scale output from the GCM. Thus, local scale (i.e. sub-GCM grid cell
111 resolution) climatic characteristics are entirely dependent upon the baseline
112 climatology used in the downscaling. If uncertainty in the baseline climatology is
113 high, this can lead to erroneous realisations of the climatic landscape, which could, in
114 turn, affect assessments of climate change impact on species. Few studies have even
115 noted the potential importance associated with uncertainty among baseline climate
116 datasets (Parra & Monahan, 2008; Roubicek *et al.*, 2010; Watling *et al.*, 2014) and no
117 studies have yet incorporated this source of uncertainty into a regional climate change
118 impact assessment (although, Baker *et al.* (2015) used multiple modelled baselines
119 simulated in a regional climate model).
120
121 The most commonly used baseline climate data are derived from observation records,
122 usually in a gridded format that represent area-based averages across grid cells, with
123 the spatial extent of cells typically between 1km^2 and 2500km^2 (Hijmans *et al.*, 2005;
124 Haylock *et al.*, 2008). Both ground-based and satellite observation data are used to

125 construct these climate baselines, though ground-based observations provide the only
126 source for long-running (pre-1970s) reconstructions. Converting these observations
127 into a coherent gridded climate product requires considerable data processing
128 (Haylock *et al.*, 2008; Hofstra *et al.*, 2009; Isotta *et al.*, 2014). Uncertainty in ground-
129 based observations may arise from differences in the density of observation stations,
130 interpolation methodology, or simple recording errors (Efthymiadis *et al.*, 2006;
131 Hofstra *et al.*, 2010). For satellite-derived observations of the climate, uncertainties
132 may be introduced when converting the retrieved electromagnetic signal to a physical
133 parameter (e.g. precipitation) or by atmospheric factors that affect the signal retrieved
134 by the satellite (Tapiador *et al.*, 2012). The methodological choices and assumptions
135 made during the downscaling process, along with error and bias in the original
136 observation data, often results in datasets that contain much uncertainty.
137
138 Here, we demonstrate variation among different historic climate baselines and explore
139 how this uncertainty affects species-climate relationships and, consequently, how this
140 impacts projections of species'(Nakicenovic *et al.*, 2000) responses to climate change.
141 We explore climate data and produce models across sub-Saharan Africa, a region with
142 a large spatial extent, that experiences a range of climate phenomena, and where
143 uncertainty in the historic climate record is high (Sylla *et al.*, 2013). Within this
144 region we examine spatial patterns in baseline climate uncertainty, where uncertainty
145 is a measure of variation among different baseline climate datasets. We evaluate the
146 consequences of this uncertainty on projections of climate change impacts for birds of
147 conservation concern (birds being the best-studied class of organisms, with
148 moderately high resolution distribution maps available for all species across the
149 region). We evaluate the impact of baseline climate variability on projections of

150 species-climate relationships, and we contrast the resultant uncertainty in model
151 projections of climate impacts on species with other measures of uncertainties that are
152 now routinely incorporated into species-climate modelling. These other sources of
153 model uncertainty arise from the choice of GCMs and SDMs, and the uncertainty
154 associated with using subsets of data for model fitting (which we term 'blocks').
155 Currently, considerable effort is made to describe uncertainty in species-climate
156 projections arising from, for example, GCM and SDM choices (Garcia *et al.*, 2012;
157 Bagchi *et al.*, 2013), but variation in the baseline climate products used to construct
158 such models has, to date, been overlooked. We contextualise the importance of
159 baseline climate uncertainty to biodiversity conservation by evaluating projected
160 changes to avian diversity across the network of Important Bird and Biodiversity
161 Areas (IBAs; the largest global network of systematically identified sites that are
162 significant for the persistence of biodiversity; BirdLife International, 2014) across
163 sub-Saharan Africa. Finally, we discuss approaches for incorporating uncertainty
164 associated with historic climate data into assessments of climate change impacts for
165 biodiversity.
166
167 **Materials & methods**
168 ***General circulation model ensemble***
169 GCMs are not equally capable of representing key regional climate phenomena, such
170 as the spatial and temporal patterns of precipitation. Here, we select an ensemble of
171 GCMs for downscaling, based on the assumption that models capable of simulating
172 past climates with some accuracy are the 'best candidates' for predicting future
173 climates (Stott & Kettleborough, 2002; Rowlands *et al.*, 2012). Thus, we selected a
174 five-member subset of a 17-member Perturbed Physics Ensemble (PPE) of the Hadley

175 Centre GCM (Gordon *et al.*, 2000; Pope *et al.*, 2000). A PPE explores uncertainty in
176 the parameterisation of the GCM by varying uncertain model parameters
177 systematically. The five-member ensemble was selected from the PPE based on the
178 criteria of realistically simulating the main features of the regional climate, and of
179 capturing a range of plausible climate outcomes (McSweeney *et al.*, 2012;
180 Buontempo *et al.*, 2014). The models were run over the global domain for the SRES
181 A1B scenario (Nakicenovic *et al.*, 2000).
182
183 ***Historic gridded climate baselines (c. 1979-2009)***
184 We selected six 'observed' gridded datasets as the historic baselines for SDM fitting
185 and for the GCM downscaling; these represented products derived from ground
186 observations, satellite observations and hybrid products (see Table 1 for full details).
187 For each dataset we obtained the mean monthly temperature (T_{mean}) and the total
188 monthly precipitation (P_{total}). In addition to readily available datasets, we also
189 combined *TRMM*, a satellite precipitation product, with the T_{mean} from CRU TS3.1, to
190 create a hybrid dataset, here named CRU.TRMM. We extracted baseline climate data
191 for the period 1979-2009, where available, in observed datasets; this permitted the
192 inclusion of satellite products. WorldClim data was only available for the period
193 1950-2000 (as a pre-processed product) and TRMM satellite data only for the period
194 1998-present. However, it was important to include these data in this analysis despite
195 the temporal mismatch due to the popularity of WorldClim and the importance of
196 TRMM for tropical precipitation monitoring. WorldClim shows very similar trends
197 and magnitudes across different regions to CRU, WFDEI.CRU and WFDEI.GPCC
198 data (Fig. 1). The magnitude of TRMM P_{total} tends to be lower than the other datasets,
199 but this is consistent with prior evaluation (e.g. comparision with CRU, Mariotti *et al.*,

200 2014) and unlikely to be due to the temporal mismatch. Each gridded climate baseline
201 was resampled onto the same grid; African CORDEX domain (longitude range = -
202 24.64, 60.28; latitude range = -45.76, 42.24; Giorgi *et al.*, 2009) at a 0.44^{o} spatial
203 resolution (c. 50km resolution).
204
205 Figure 2 shows the spatial patterns of the uncertainty in climate observation datasets
206 for each season, for precipitation and temperature. Temperature uncertainty is shown
207 by the range of values (degrees Celsius) across the climate observations. Precipitation
208 uncertainty is shown by the coefficient of variation, calculated on the observed
209 climate datasets. For the latter, we excluded areas where the total seasonal
210 precipitation was less than 30mm. The 30mm threshold was intended to remove very
211 arid areas, which may have only 1 or 2 short duration, but intense, rain events per
212 year. In these locations, the 3-hourly repeat cycle of TRMM may be insufficient to
213 identify the rainfall event. This means that there is a greater chance of the satellite not
214 capturing the climate correctly in comparison with rain gauge measurements that
215 capture the accumulated precipitation over one hour. Such a discrepancy creates an
216 unrealistically high standard deviation in the mean, which no longer reflects
217 differences in the observed quantities.
218
219 For modelling species distributions, we derived four bioclimate variables that showed
220 low colinearity (correlation coefficients <0.7) and that have been related previously to
221 species distributions (Barbet-Massin & Jetz, 2014). Bioclimatic variables are widely
222 used in SDM analyses, and aim to describe biologically important aspects of climatic
223 variation (Busby, 1991). We calculated the mean of T_{mean} and P_{total} for each month
224 across the 30-year baseline time period, and used these to calculate the four

bioclimate variables: annual total precipitation (annual sum of P_{total}); annual mean temperature (annual mean of T_{mean}); precipitation seasonality (coefficient of variation of P_{total}); and temperature seasonality (standard deviation of T_{mean} x 100). From this point, we refer to these climate baseline datasets as CLIM.

Downscaling GCM simulations

The five GCM simulations were each downscaled using the CFM following the method of Tabor & Williams (2010), in which the monthly absolute anomaly for each variable (from GCMs) was calculated between the baseline period (c. 1979-2009) and the two future focal periods (2040-2069; 2070-2099). This anomaly was then regridded to 0.44 degrees spatial resolution using cubic spline interpolation, and added to the observed T_{mean} and P_{total} for the baseline period to produce projections of future climate. This process was carried out using each of the six gridded CLIM datasets, to produce 30 climate projections (5 GCMs x 6 CLIM) of future climates for each time period. The bioclimate variables described above were then calculated for each future time period and projection.

Species distribution modelling

For the analysis, we selected bird species of conservation concern (BirdLife International, 2015) that have their entire breeding range within the African CORDEX domain (n = 925). The latter criterion ensured that we could model the entire species-climate response. Species of conservation concern include those classified as threatened, restricted-range, biome-restricted or congregatory species (those that trigger criteria for identifying IBAs; BirdLife International, 2014). These species were included in order to be representative of those typical of impact assessments (e.g.

250 Hole *et al.*, 2009; Bagchi *et al.*, 2013). Species distribution data were derived from
251 refined species distribution maps from BirdLife International & NatureServe (2013).
252 These distributions were gridded onto a regular grid across Africa, to match the
253 resolution of the climate data (0.44 degree resolution). A species was considered to
254 occur in a cell if the distribution polygon overlapped ≥10% of the cell, which is a
255 liberal threshold that helps ensure that species with restricted ranges are represented.
256 Due to a lack of true absence data, and because all areas beyond the range extent are
257 extremely unlikely to contain false absences, for modelling we consider all cells
258 beyond the range to be true absences.
259
260 We used a jack-knife approach to model the distribution of each species, that aimed to
261 capture the contribution of several sources of uncertainty in projected species'
262 responses to future climate conditions, and closely follows Bagchi *et al.* (2013) and
263 Baker *et al.* (2015). The principle of the approach is to build a model using different
264 combinations of data and modelling techniques (i.e. potential sources of uncertainty),
265 and to use the variability in the resulting models to identify the contribution of each
266 potential source of uncertainty to assessments of species' responses to climate change.
267
268 Firstly, the region was divided into six spatially disaggregated blocks for model
269 building/testing (see Bagchi *et al.* 2013 for full description of blocking method). In
270 brief, the blocking approach involves dividing the region into small subunits and then
271 grouping these into six spatially disaggregated blocks, such that the mean and
272 variance of each bioclimatic variable was approximately equal across the blocks
273 (using Blocktools package in R). In model building/testing, models were built on each
274 combination of five blocks and tested on the omitted block. This protocol: (1) reduces

the potential confounding effect of spatial autocorrelation in both cross-validation and the assessment of model performance (unlike random k-fold partitioning); (2) maintains similar parameter space (e.g. the numeric range of climatic variables) in all model building and testing procedures; and (3) can be used to assess the effect of spatial autocorrelation on projected impacts.

For each species, we modelled the statistical relationship between the species' distribution and the four bioclimate variables, calculated for each of the six CLIM datasets, using each of four SDM techniques (Generalised Linear Models, GLMs; Generalised Additive Models, GAMs; Generalised Boosted Models, GBMs; Random Forests, RFs) for each of the six combinations of five blocks. For each species, a maximum of 144 models could be built, with each jack-knife combination of GCM, SDM, CLIM and block. The median area under the receiver operating characteristic curve (Area Under Curve; AUC) from across the six blocks was used to assess final model accuracy for each species, SDM, GCM and CLIM combination. The median AUC was consistently high (0.98; 95% quantiles = 0.84, 1.00). The model cross-validation procedures used to optimise each model follows Bagchi *et al.* (2013). Models were not run for a species where an excluded block contained no presences, which meant this block could not be used for cross-validation (see Bagchi *et al.* 2013). All species with breeding ranges occupying fewer than 10 cells were also omitted from the analysis due to difficulties in modelling such sparse data. From the 925 species of conservation concern, 895 had sufficiently large range extents to be included in the final analysis.

Projections of contemporary climate suitability across the entire region were made for each species and each model, by applying models to the same CLIM dataset as used for training. Projections were made to the baseline period, so that future suitability could be assessed relative to the modelled baseline suitability for consistency. Each model was used to project future suitability for a species, applying the model to the future climate projection downscaled using the same baseline climate data used in model building. For each species and time period, this resulted in a maximum of 720 future projections (CLIM [6] x GCM [5] x SDM [4] x block [6]).

The importance of baseline climate uncertainty to projected impacts

We assessed the importance of baseline climate (CLIM) uncertainty to overall uncertainty in the context of two commonly employed metrics of climate change impacts on species: species turnover and change in species-specific climate suitability. We calculated the projected species turnover in each cell for each projection combination using the Bray-Curtis index, a measure of dissimilarity between two communities. Species turnover is commonly used in climate change impact studies as a way of representing projected change in community composition through time (Hole *et al.* 2009; Buisson *et al.* 2010; Bagchi *et al.* 2013). Species turnover ($T_j[t_f]$) for each cell *j* was calculated between the t_0 = baseline (c. 1979-2009) and t_f = future (2040-69 or 2070-2099) from projected climate suitabilities as:

$$T_j\left[t_f\right] = \frac{\sum_{k=1}^{S} |P_{jk}[t_f] - P_{jk}[t_0]|}{\sum_{k=1}^{S} P_{jk}[t_0] + \sum_{k=1}^{S} P_{jk}[t_f]} \quad \text{Eq. 1}$$

where, P_{jk} = suitability of species *k* in cell *j,* and *s* is the total number of species. This resulted in 720 projections of species turnover for each cell and time period.

The variability in projected turnover was partitioned out between the potential sources of uncertainty (GCM, SDM, CLIM and block) by modelling projected species turnover (values bounded between 0 and 1) within each cell as a function of the four potential sources of uncertainty, using generalised linear models with binomial error distribution and logistic link function. We then dropped each factor in turn from the full model and assessed the contribution of each factor to overall uncertainty (Buisson *et al.*, 2010) as:

$$P_f = \frac{D_f - D_1}{D_0} \times 100 \qquad \text{Eq. 2}$$

where, P_f = percentage of deviance explained by factor *f*, D_1 = deviance of full model, D_f = deviance of full model minus factor *f*, and D_0 = deviance of null model (intercept only). Deviance is approximately equivalent to sums of squares for generalised linear models. The percentage of deviance explained by each factor in each cell was mapped and the results presented in Fig. 3.

The change in the summed climate suitability (S_k) for each species (*k*) between the baseline period and each future period, which provides an index of overall change in suitability for a species, was calculated separately for each of the (max.) 720 species-specific future projections. The change in climate suitability for each of these projections is simply the summed climate suitability across all cells for the future period, minus the summed climate suitability across all cells for the appropriate baseline projection. The variability in projected S_k was partitioned following the

348 above approach, but using a general linear model, assuming Gaussian errors, and with
349 an identity link (Fig. 4).
350
351 ***Baseline climate uncertainty in a conservation context***
352 To contextualise the contribution of baseline climate (CLIM) uncertainty to climate
353 change impact assessments, we projected species turnover within African sub-Saharan
354 IBAs for the 2070-2099 period. We used an approach that aims to avoid the high
355 uncertainty that occurs when climate data is downscaled to very high resolutions for
356 assessment of climate change impact in small spatial areas, such as protected areas
357 (Hole *et al.*, 2009; Bagchi *et al.*, 2013). Thus, we use species-specific climate
358 suitabilities at the resolution of the climate projections, here 50km, and assume that
359 the suitability within an IBA is broadly characterised by the suitability of the cell(s) in
360 which the IBA is embedded. The methodology follows that of Baker *et al.* (2015).
361 Thus, species turnover was calculated (using Eq. 1, but redefining j = IBA) for each
362 IBA using a weighted mean of the species-specific climate suitability for the cell(s)
363 that are intersected by the IBA, with weights equal to the percentage of the IBA's
364 extent that overlaps the cell(s). Turnover was calculated separately for each of the 720
365 jack-knifed combinations, and then the ensemble mean species turnover for each IBA
366 was calculated for each set of projections built using the same CLIM. This is similar
367 to Hole *et al.* (2009), where the mean across climate projections was calculated.
368
369 We use the ensemble mean projected turnover for models built using CRU climate
370 data as a reference projection with which to compare turnover from the other
371 ensemble projections made using different CLIM datasets. To visualise the impact of
372 using different CLIM datasets to create a projected ensemble turnover estimate, for all

six CLIM ensembles we assign turnover values for IBAs to one of five percentile categories (0-20%, 21-40%, 41-60%, 61-80%, 81-100%). We then summarise turnover differences between projections based on the CRU baseline dataset and those based on each of the other CLIM datasets, in terms of shifts between turnover categories. This is important because climate change impacts are often presented in such a categorical or absolute fashion (i.e. without a measure of uncertainty), but shifts between categories due to underlying uncertainty could drastically alter perceptions of climate change vulnerability.

Results

Variability among historic gridded baseline climate datasets

The observed annual cycle for the period c. 1979-2009 varied considerably between observational datasets for P_{total} (Fig. 1); however, similar variations were not found for T_{mean}. For precipitation, all observational datasets in all regions showed agreement on the timing of precipitation peaks, but the P_{total} varied considerably between datasets. This difference was most pronounced for the TRMM and UDEL datasets in the West Sahel, West Tropical and Southern Africa regions, although P_{total} for the CRU, WorldClim and WFDEI datasets were very similar. The spatial distribution of disagreement between precipitation datasets (Fig. 2a), shown by the coefficient of variation, revealed that the main locations of disagreement between precipitation datasets are in the Sahel between September and November, and southern and eastern Africa in March to May and September to November.

The spatial distribution of disagreement between temperature observations (Fig. 2b), shown by the T_{mean} range between observations, did not show large differences

between seasons. In this case, the locations of large disagreement tended to be confined to small areas in the Namib Desert, semi-arid savannahs, or East African montane environments. This highlights the potential for considerable variability between baseline climatologies.

The importance of baseline climatology in climate change impacts assessments

Uncertainty in species turnover attributable to choice of baseline climate data (CLIM) was high for both time periods (Fig. 3; median 2040-2069 = 15.9%; 2070-2099 = 16.5%), and was comparable in magnitude and importance to GCM choice (19.1%; 22.2%). The largest source of uncertainty in species turnover across the region was attributable to SDM choice (37.5%; 31.4%), the importance of which decreased by 2070-2099, but remained dominant. In both time periods all three main sources of uncertainty (SDM, CLIM, GCM) affected species turnover estimates. Uncertainty in projected turnover attributed to variability associated with using different data subsets (blocks) was consistently low.

Across the region, the dominant source of uncertainty in species turnover was highly spatially variable, and in many areas multiple sources were simultaneously important (Fig. 3). By the end-of-century, uncertainty associated with CLIM was highest in southern Africa, and in parts of the western Sahel (e.g. Senegal and Gambia). GCM uncertainty dominated across parts of Eastern Africa, and became more important in parts of the Sahel and montane areas by the end-of-century. Uncertainty in turnover associated with SDM choice was spatially distributed across much of the region in both time periods, and showed several areas where this source of uncertainty was overwhelmingly dominant.

Uncertainty in the change in climate suitability (S_k) for individual species attributable to the use of different CLIM datasets was, on average, almost twice as important as variation due to GCM choice (Fig. 4; median 2040-2069=12.1% vs. 6.5%; 2070-2099=10.4% vs. 4.6%), although there was considerable variation across species. The uncertainty attributed to SDM methodology was almost double that attributable to CLIM, and four times that attributable to GCM, in both time periods (median 2040-2069=22.4%; 2070-2099=24%), but CLIM remained a much more important source of uncertainty than GCM, or that associated with using different data subsets (block). The species for which CLIM is a dominant source of uncertainty (Fig. 5) occur principally in areas of where CLIM variability was indicated to be high (e.g. Atlantic coastal regions in the sub-tropical zone) and also areas that are remote and have few weather stations (e.g. Sahel; see Fig. 2).

The importance of baseline climatology in a conservation context

The choice of CLIM dataset can impact upon projected species turnover across areas of conservation value, substantially altering projected climate change impacts (Fig. 6). For example, changing the source of precipitation data from ground observations to satellite derived products (e.g. CRU [Fig. 6a] vs. CRU.TRMM [Fig. 6b]), but using the same temperature data, increases the severity of projected turnover across most of the continent. Conversely, species turnover derived from models built on WFDEI.CRU baseline data projected similar (or lower) species turnover than those made using CRU climate data. Comparing models derived from CRU versus UDEL data, less severe turnover was projected for some montane IBAs (e.g. Ethiopian Highlands) using UDEL data, but higher turnover was projected elsewhere. Thus, the

choice of baseline climate data had a notable impact on projections of climate change impact for sites of conservation relevance.

Discussion

Here we have demonstrated that the choice of historic baseline climate data can have substantial and important impacts on projected responses of species and communities to future climate change. This is an almost universally overlooked source of uncertainty, but could severely affect projected responses of species to climate change, with significant consequences for conservation prioritisation and management. We found that the choice of baseline climate data affects the overall uncertainty in climate change impacts (measured as species turnover and change in species-specific climate suitability) to a degree comparable with the choice of GCM data. The literature on projecting species' responses to climate change is dominated by calls to consider uncertainty arising from the choices of GCMs, SDMs and climate predictors (Elith & Graham, 2009; Synes & Osborne, 2011; Garcia *et al.*, 2012), as well as spatial autocorrelation (Dormann *et al.*, 2008; Bagchi *et al.*, 2013). This has resulted in the widespread use of ensemble models to average across, or more recently, to quantify uncertainty (Bagchi *et al.*, 2013; Baker *et al.*, 2015). Yet here we provide evidence that the choice of baseline climate data (CLIM) is at least as important as previously identified sources of uncertainty. Importantly, the three dominant sources of uncertainty tested here show idiosyncratic spatial patterning in their importance. For example, uncertainty associated with CLIM was consistently highest in Southern Africa and parts of Western Africa.

In agreement with previous studies (e.g. Buisson *et al.*, 2010; Garcia *et al.*, 2012; Bagchi *et al.*, 2013), choices in SDM methodology and GCM data contribute substantially to the uncertainty in projected species turnover, dominating in many regions. Uncertainty due to differences in the modelled species-climate response using different SDM methodologies is a well-established source of uncertainty in SDM analyses (Elith & Graham, 2009), and is one of the primary reasons for using ensembles of models (Araújo & New, 2007). Without truly independent data for evaluating the predictive performance of these different modelling algorithms it is difficult to select a single best approach, and this makes it highly important that the uncertainty associated with these methodological choices is explored and quantified (Baker *et al.*, 2015). It should also be noted that overall uncertainty in projected impacts based on correlative models is likely to be overly narrow. In a meta-analysis of projected extinction risk, Urban (2015) found that mechanistic and correlative models projected the lowest extinction risk, while species-area relationship models and expert opinion had substantially higher extinction risks.

Figure 1 shows important differences between the observational datasets, especially with regard to precipitation. While the month of seasonal minima and maxima are generally in agreement across all datasets, there are considerable discrepancies between monthly precipitation totals – differences that are also supported by Nikulin *et al.* (2012). These differences are most evident between the TRMM, UDEL and other synoptically derived datasets (CRU, WFDEI.CRU, WFDEI.GPCC and WorldClim), and can be mostly explained by variations in sources of synoptic observations and methodological differences. To some extent these differences should not come as a surprise, as CRU, GPCC and WorldClim datasets have provenance

497 from synoptic weather reports by National Meteorological and/or Hydrological
498 Services (NMHSs) to the World Meteorological Organisation (WMO) Global
499 Telecommunication System (GTS). While the UDEL dataset is also derived from
500 synoptic observations, it has provenance from different databases (National Oceanic
501 and Atmospheric Administration's (NOAA) Global Historical Climatology Network
502 (GHCN) version 2, and the National Climate Data Center's (NCDC) Global Surface
503 Summary of the Day (GSOD), as well as other national level data). The quality
504 control, processing steps, interpolation methods and evaluation methods are all
505 potentially additional factors that could explain the differences found between UDEL
506 and the other synoptically derived datasets.
507
508 Variation in turnover projections associated with GCM uncertainty was important in
509 some regions, particularly in the East Africa. However, it is surprising that the relative
510 importance of GCM uncertainty was not higher, given the considerable variability in
511 climate anomalies among these GCMs (Buontempo *et al.*, 2014), and the range of
512 uncertainty associated with GCMs used in other assessments (e.g. Garcia *et al.*, 2012).
513 The GCM ensemble used in this study was composed of a subset of models that were
514 able to simulate well observed climate phenomena across the region, but was also
515 selected to represent the range of responses to climate forcing, as found in a larger
516 multi-model ensemble. Thus, despite the considerable uncertainty across this
517 ensemble, the uncertainty is likely to be narrower than ensembles used in many
518 studies, due to the omission here of regionally implausible GCMs (McSweeney *et al.*,
519 2014). Few studies justify the selection of GCMs and provide an assessment of their
520 ability to capture the historic climatology of the focal region (Baker *et al.* 2015). More

521 careful consideration of the GCMs selected might reduce unwarranted uncertainty
522 (McSweeney *et al.*, 2012, 2014).
523
524 Here we demonstrate spatial heterogeneity in the importance of potential sources of
525 uncertainty, and that no one source consistently dominates. This has important
526 consequences for regionally focused impact studies, where regional characteristics
527 associated with baseline climate data availability could alter the importance of
528 different sources of uncertainty. Differences in baseline climatologies could arise
529 from differences in the selection of climate data (e.g. difference subsets of stations,
530 use of satellite data, different interpolation algorithms) and the spatial variability of
531 climatic conditions (e.g. high variability over mountainous or coastal areas). The
532 importance of this uncertainty for individual species might be dependent on the
533 characteristics of their range (see Fig. 2 and Fig. 5). Species with ranges that
534 encompass high orographic variation, and span areas with low densities of climate
535 observation data, are likely to be particularly affected by baseline uncertainty (e.g.
536 Hofstra *et al.*, 2010). Such regions in Africa might include topographically diverse
537 regions such as the Albertine Rift Valley, and montane ecosystems such as the
538 Ethiopian and Cameroon Highlands. Additionally, sparsely populated regions, such as
539 the Saharan and Sahelian biomes, have low densities of weather observation records
540 and are likely to be particularly affected by climate baseline uncertainty (e.g. Sylla *et*
541 *al.*, 2013).
542
543 Several other sources of uncertainty that are not explored in this study are likely to be
544 important for projecting species' responses to climate change. Most notably, the
545 choice of climate predictor variables has been shown previously to have a large effect

546 on the projected distribution (Synes & Osborne, 2011; Braunisch *et al.*, 2013). The
547 relative importance of the choice of predictor variables is likely to be high, and in
548 future should be assessed in the context of the wider uncertainty, as has been done
549 here for baseline climate uncertainty. However, it is important to make sure that the
550 range of uncertainty is realistic by including only biologically plausible combinations
551 of climate predictors (Synes & Osborne, 2011).
552
553 This study has focused on a region that, overall, has a low density of weather
554 observations (Sylla *et al.*, 2013), especially when compared to parts of, for example,
555 Europe and North America (for example, Hijmans *et al.* 2005). However, weather
556 stations across the globe are patchily distributed, and typically reach the highest
557 densities in areas of importance for human populations. Thus, in more remote
558 locations, many of which are likely to be of higher importance for biodiversity,
559 weather observations densities are likely to be low. Even where high densities of
560 weather stations occur, careful consideration should be given to the variation in local
561 climate. Factors that are likely to reduce the correlation in observations between
562 neighbouring weather stations, such as topographically complex terrain or coastal
563 features, might suggest that baseline uncertainty should be considered. The
564 conclusions of this study are likely to apply broadly to most ecological studies
565 involving climate data, but will be most problematic in areas where the density of
566 observation data is low compared to the spatial variability of the local climate.
567
568 Correlative species distribution models are frequently used to assess the potential
569 impacts of climate change in networks of protected areas or sites of biodiversity
570 importance (Hole *et al.*, 2009; Araújo *et al.*, 2011; Bagchi *et al.*, 2013; Baker *et al.*,

571 2015). Adaptation plans are informed by such projections and, consequently, it is
572 important to understand the sensitivity of projected impacts to choices made during
573 the modelling process. As we have shown, projected impacts across IBAs can be
574 altered considerably by simply choosing different baseline climatology to correlate
575 with a species' distribution. Rather than simply mapping impacts based on the
576 ensemble average (which is common practice: e.g. Hole *et al.*, 2009; Araújo *et al.*,
577 2011; Bagchi *et al.*, 2013), we advocate representing the degree of uncertainty in
578 spatial maps to better communicate the degree of confidence in projected impacts
579 (Baker *et al.*, 2015).
580
581 Uncertainty in baseline climate data has relevance beyond species distribution
582 modelling. It will be important in any situations where uncertainty in the historic
583 record has the potential to undermine inferences, such as studies analysing ecological
584 responses to inter-annual climate variability (VanDerWal *et al.*, 2013), phenological
585 studies (Phillimore *et al.*, 2012) and climate impact indicators (Gregory *et al.*, 2009).
586 There are several ways to incorporate uncertainty in baseline climate into models of
587 species-climate responses. Uncertainty can be explored, as here, by using multiple
588 historic baselines, or alternatively, exploring the impact of uncertainty within a
589 historic climate dataset using stochastic simulations that assume each variable has an
590 associated random error (Folland *et al.*, 2001; Brohan *et al.*, 2006). Estimates of these
591 error distributions are often generated along with the estimated climatology by, for
592 example, leaving single observations out of the interpolation and assessing the
593 difference between observed and predicted values (e.g. Hijmans *et al.* 2005). Some
594 climate products consider a broad range of climate uncertainty, including
595 measurement errors, homogenisation uncertainty and sampling errors (e.g. Brohan *et*

596 *al.* 2006). Recent advances in modelling allow for the explicit inclusion of uncertainty
597 associated with environmental predictor variables, and these approaches could be
598 used to incorporate uncertainty in the climate data into modelled species-climate
599 responses (Stoklosa *et al.*, 2015). Our findings should encourage greater consideration
600 of uncertainty associated with historic baselines when assessing potential responses of
601 species to climate change. Indeed, considerations of uncertainty in historic baseline
602 data should become routine for all research incorporating such data (Parra &
603 Monahan, 2008).
604
605 To conclude, we have shown that projected responses of species to climate change
606 can be highly affected by uncertainty in the historic climate baseline data used to
607 model species-climate relationship in SDM analyses and to downscale GCM data
608 from coarse resolutions to ecologically relevant spatial scales. From our results it is
609 evident that ecological studies should begin to routinely account for this source of
610 uncertainty. Within a conservation context, this will facilitate better planning for
611 targeting monitoring and adaptation interventions, and help strengthen conservation
612 efforts in the face of a rapidly changing climate.
613
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617 anonymous reviewers, which helped greatly to improve the clarity of the manuscript.

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807

808 Table 1. Historic gridded climate datasets (CLIM) used in SDM fitting and downscaling GCM simulations of future climates using the change
809 factor method (CFA). The TRMM precipitation dataset was combined with the temperature variables from CRU TS3.1 to create CRU.TRMM
810 used in the analysis.

811

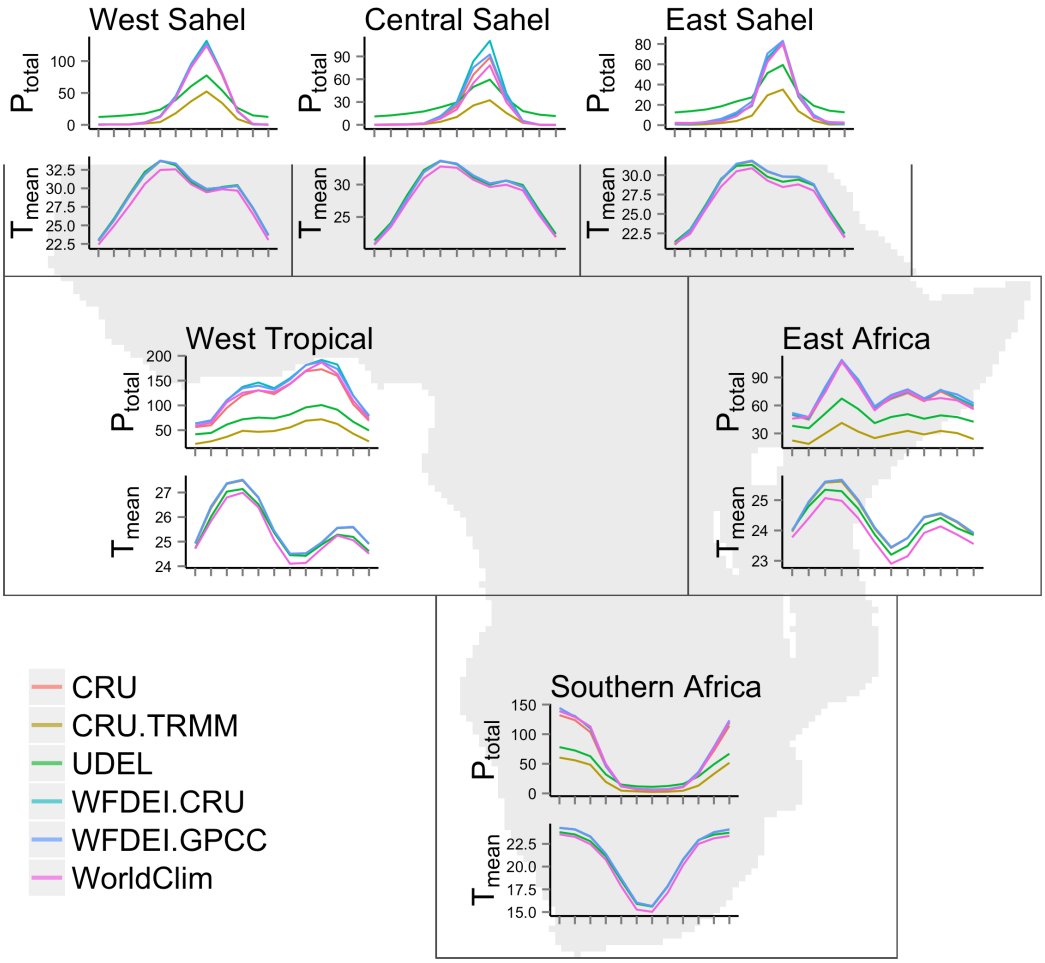
Dataset	Variables	Time period	Spatial resolution	Description	References
CRU TS3.1	T_{mean} P_{total}	1900-2012	0.5^0	Time series of spatially interpolated monthly observations from meteorological stations	(Harris *et al.*, 2014)
TRMM	P_{total}	1998-present	0.25^0	Satellite observations, calibrated using rain gauge data	(Huffman *et al.*, 2007)
WFDEI.CRU	T_{mean} P_{total}	1979-2012	0.5^0	ERA-Interim reanalysis data elevation and bias corrected using CRU TS3.1	(Weedon *et al.*, 2014)
WFDEI.GPCC	T_{mean} P_{total}	1979-2012	0.5^0	ERA-Interim reanalysis data elevation and bias corrected using GPCC	(Schneider *et al.*, 2014; Weedon *et al.*, 2014)
WorldClim	T_{mean} P_{total}	1950-2000	0.167^0	Spatially interpolated monthly mean observations from meteorological stations for 1950-2000	(Hijmans *et al.*, 2005)
UDEL	T_{mean} P_{total}	1900-2012	0.5^0	Time series of spatially interpolated monthly observations from meteorological stations	(Legates & Willmott, 1990; Willmott & Robeson, 1995)

812 Figure 1. Summary of mean monthly total precipitation (P_{total}, mm/month) and
813 monthly mean temperature (T_{mean}, ^{o}C) for the period c. 1979-2009 for six regions of
814 sub-Saharan Africa (demarcated by solid lines) derived from six baseline climate
815 products (see legend and Table 1). The mean climate for each focal region is
816 calculated from the mean monthly 30-year (although see methods for details on
817 temporal periods) average of the variables in each of the cells across the region. The
818 x-axis tick marks represent the twelve months of the year, ordered from January to
819 December.
820
821 Figure 2. Spatial patterns of the uncertainty in climate observation datasets for
822 precipitation (a) and temperature (b), shown for each season (DJF: December,
823 January, February; MAM: March, April, May; JJA: June, July, August; SON:
824 September, October, November). Precipitation uncertainty is shown by the coefficient
825 of variation, calculated on the observed climate datasets (n=6). Areas of total seasonal
826 precipitation less than 30mm were removed from the analysis in order to exclude
827 areas where the standard deviation was much greater than the mean (see Methods for
828 full details). Temperature uncertainty is shown by the range of values in degrees
829 Celsius, across the climate observations (n=4).
830
831 Figure 3. The percentage of the total variability (deviance) in species turnover
832 explained by each uncertainty factor - a measure of the relative importance of each
833 factor to the overall uncertainty in projected climate change impacts across the region.
834 Changes are measured between the baseline period of c. 1979-2009 and each of two
835 focal time periods, 2040-2069 (top) and 2070-2099 (bottom). SDM = species
836 distribution model; CLIM = climate baseline data; GCM = general circulation model;

837 block = uncertainty due to using different data subsets. Note: block was included in
838 the analyses but its uncertainty was not mapped due to its minimal effect.
839
840 Figure 4. The percentage of the total variability (sums of squares) in species-specific
841 change in climate suitability, measured between the baseline period of c. 1979-2009
842 and each of two focal time periods, 2040-2069 (top) and 2070-2099 (bottom),
843 explained by each uncertainty factor (the latter as in Figure 3). The boxplots
844 summarise the importance of each sources of uncertainty across all species included
845 in the analysis *(n* = 895).
846
847 Figure 5. The pattern of species richness for species where climate baseline data
848 uncertainty (CLIM) was a dominant source of uncertainty (upper 5th percentile of
849 CLIM affected species, *n* = 48). The patterns reflect known areas of climatic
850 complexity (see Fig. 2).
851
852 Figure 6. The ensemble mean projected species turnover (by 2070-2099) for the
853 region's Important Bird and Biodiversity Areas (IBAs) for: (a) projections derived
854 from models built using CRU climate baseline data; and (b-f) the number of turnover
855 categories (percentage species turnover: 0-20%, 21-40%, 41-60%, 61-80%, 81-100%)
856 by which the projections are shifted when projections are derived from models built
857 on one of the other five climate baseline (CLIM) datasets. Thus, IBAs in plots b-f that
858 are coloured green decrease one category, and are therefore projected to have lower
859 species turnover in comparision to CRU-based projections. Similarly, IBAs in plot b-
860 f coloured red or dark red increase one or two categories, respectively, and are

861 therefore projected to have higher species turnover in comparision to CRU-based
862 projections.

863 Figure 1



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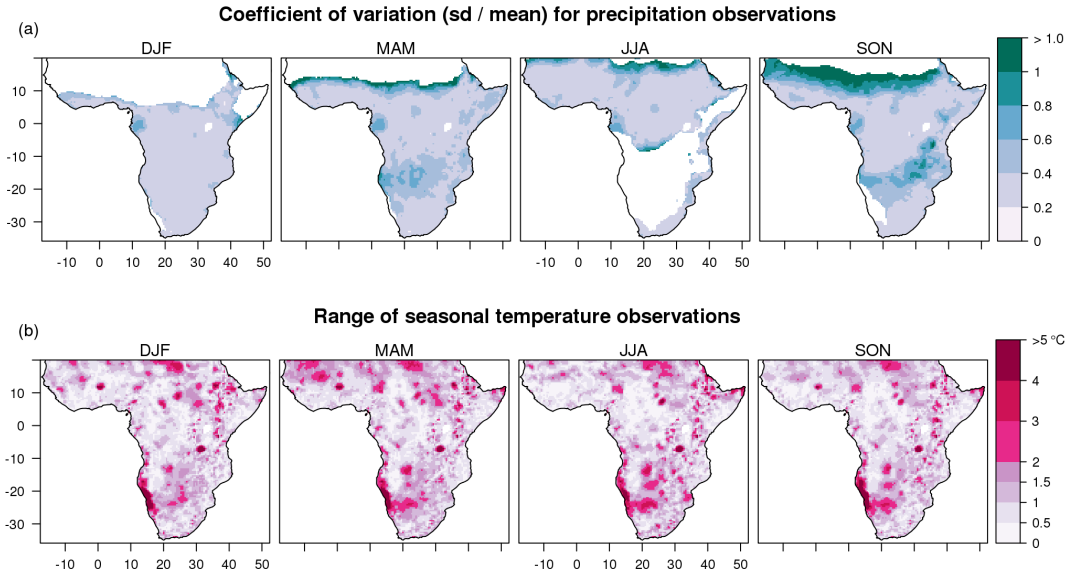
865

866 Figure 2



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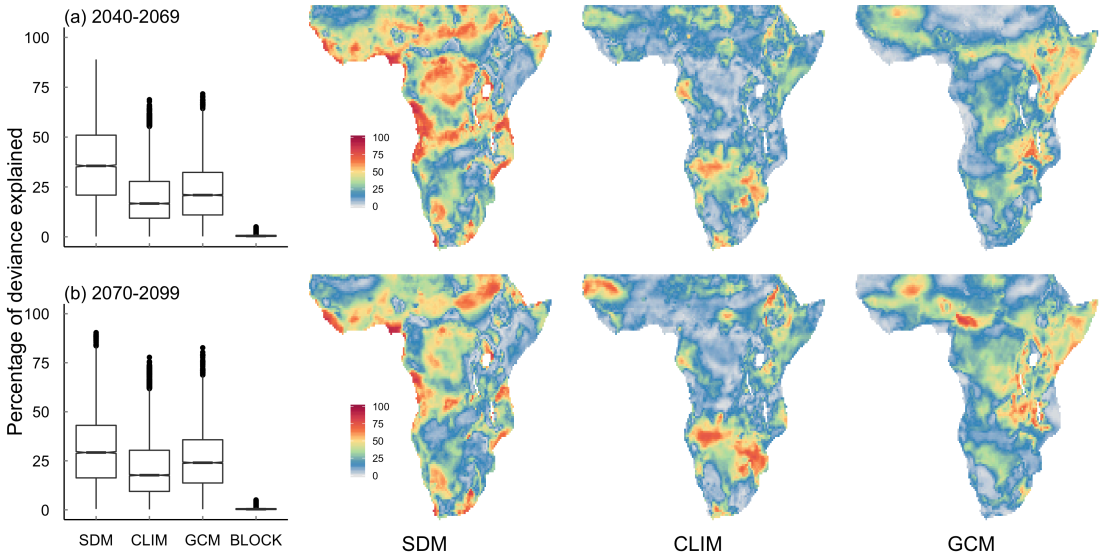
869 Figure 3



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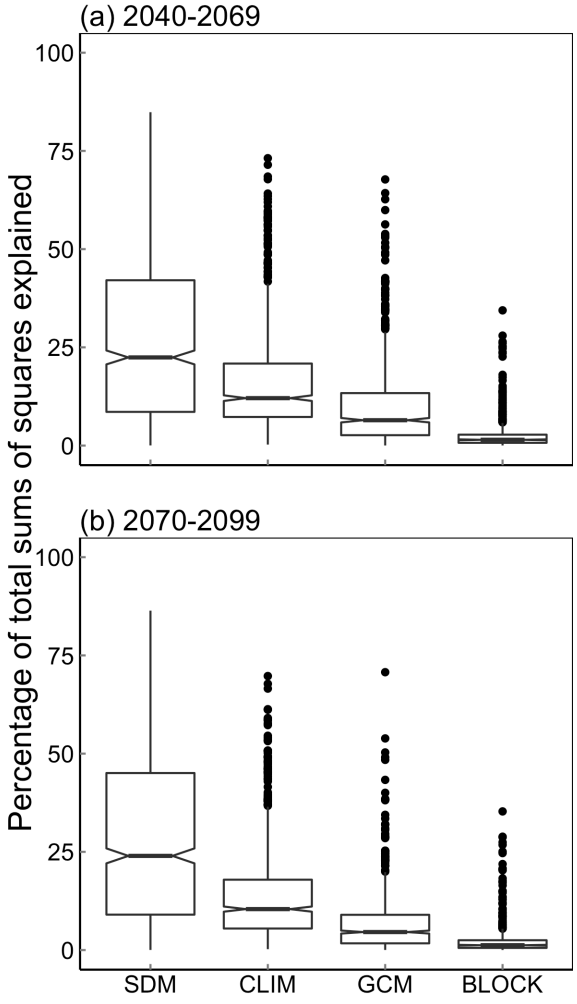
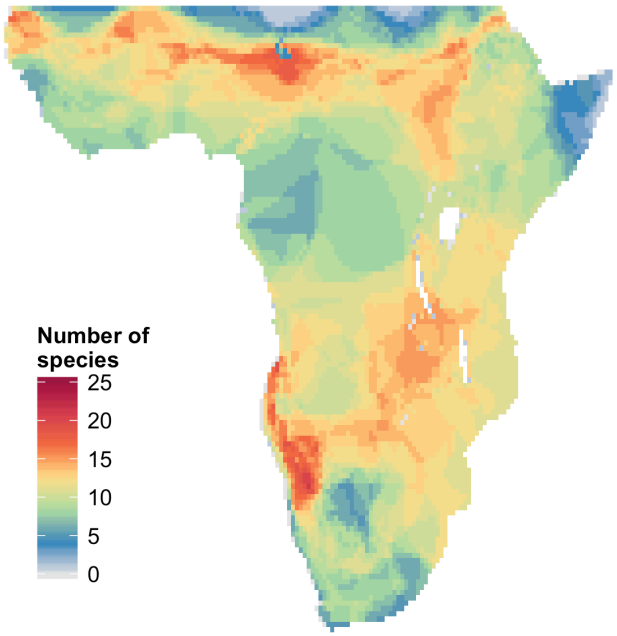
872 Figure 4



873

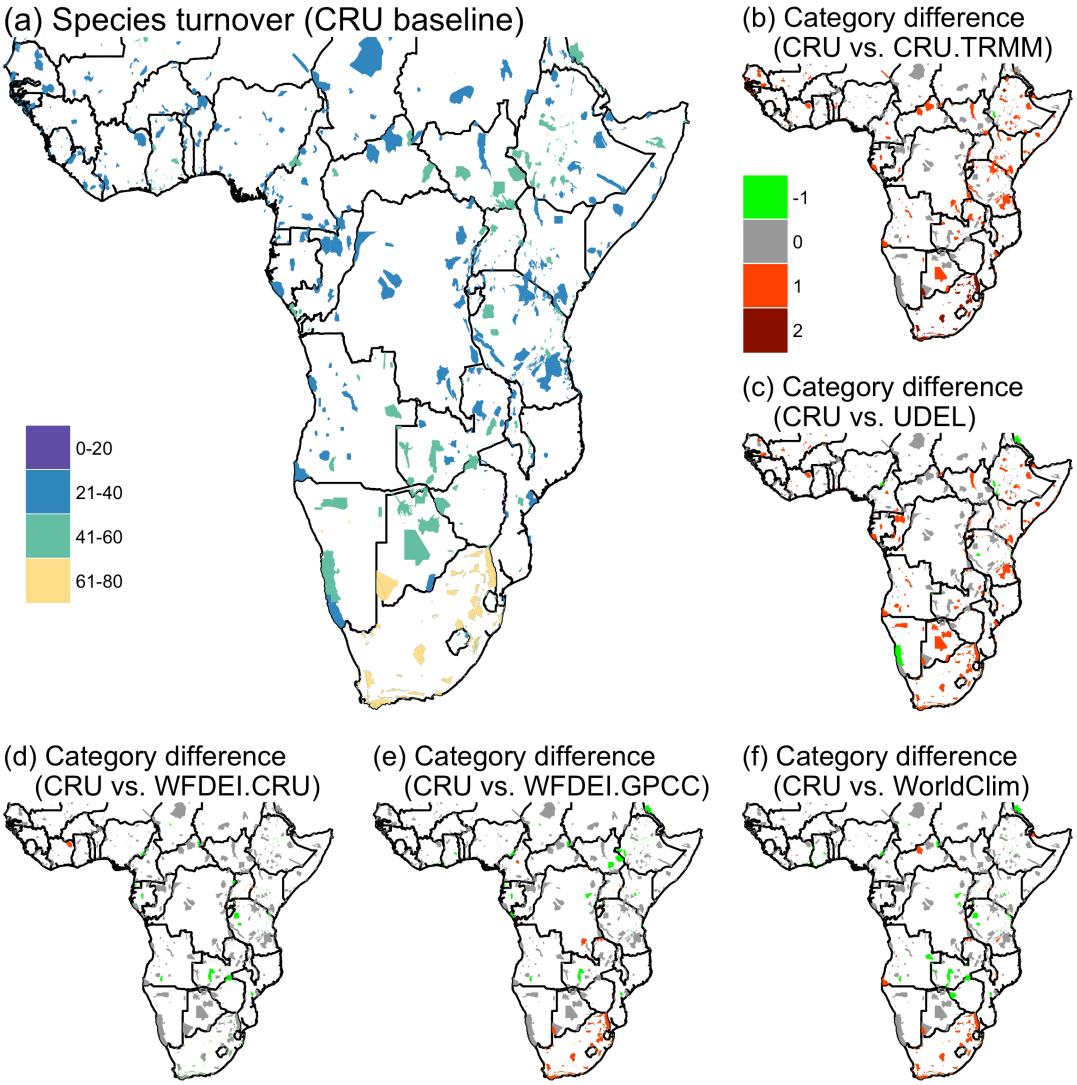
874 Figure 5



875

876

877 Figure 6



878